Development and Survivorship of Immature Angoumois Grain Moth (Lepidoptera: Gelechiidae) on Stored Corn

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ABSTRACT Life history of immature Angoumois grain moths, *Sitotroga cerealella* (Olivier), was studied on dent corn (Pioneer 3320) at 10, 15, 20, 25, 30, 35, and 40°C and at 43, 53–61, 75–76, and 82–87% RH under laboratory conditions. At 10 and 40°C, none of the stages survived at any relative humidity. Temperature was the main factor affecting egg incubation period, larval-pupal development time, and egg and larval-pupal survivorship. The shortest egg development times occurred at temperatures of 30°C and higher, but they increased sharply as temperature decreased. Larval-pupal development time was shortest at 30°C. Survivorship was optimal at 20–30°C for eggs and larvae-pupae, but larval-pupal survivorship decreased sharply at 15 and 35°C. Duration of larval-pupal development did not vary with sex. Newly emerged females were twofold heavier than males, and temperature and relative humidity did not affect weight. Sex ratio of emerging adults did not differ from 1:1 at any temperature or relative humidity. The optimum conditions for development of Angoumois grain moth on corn were 30°C and 75% RH. The data will be useful for determining safe storage conditions for corn and for developing a computer model for simulating population dynamics of immature *S. cerealella*.

KEY WORDS life history, *Sitotroga cerealella*, corn, modeling, survivorship

THE ANGOUMOIS GRAIN MOTH, *Sitotroga cerealella* (Olivier), is a cosmopolitan pest of stored corn (Arbogast and Mullen 1987), wheat (Storey et al. 1982, Imura and Sinha 1984), rice (Cogburn 1974), barley (Singh et al. 1977), sorghum (Shazali and Smith 1985), and other cereals (Bitran et al. 1978, Seifelnasr and Mills 1985), and it also attacks cereals in the field before harvest (Agrawal et al. 1977, Singh et al. 1978, Howlader and Matin 1988). This insect develops within grain kernels, causing considerable direct damage, as well as making the grain a more suitable medium for reproduction of secondary insect pests (Weston and Rattlingourd 2000). Despite the importance of this pest, quantitative data describing its life history over a range of environmental conditions at which it will develop are lacking. Such data can be used to define optimal storage conditions to reduce the level of infestation and damage by pests (Throne 1994) and to develop simulation models for optimizing pest management strategies (Throne 1995).

The Angoumois grain moth deposits its eggs singly or in groups on or near grain, and newly hatched larvae burrow into the kernels or enter through cracks in the pericarp. Larval-pupal development is completed within the kernel, and pupation occurs in a silk-lined chamber in the burrow. Before pupation, the larva cuts a channel to the outside, leaving only a weakly fastened flap of pericarp through which the adult moth will emerge (Arbogast and Mullen 1987). The life cycle of this insect varies with temperature, relative humidity, and diet. Shazali and Smith (1985) reported that total development time of this insect, from egg to adult, was completed in 25 d when reared in sorghum at 30°C and 70% RH. Total development time was 28 d when the insects were reared on corn kernels mixed with some flour at 30°C and 80% RH (Grewal and Atwal 1967) and 36 d when the insects were reared in corn at ambient temperature and relative humidity (Koone 1952).

Life history data for insects often do not include information on the effect of extreme conditions, where development or longevity is quite protracted or where survival is normally low. Often these two responses are linked. Properly stored commodities may seldom reach optimal conditions for insect growth. For example, corn stored in South Carolina was below 20°C for 55–85% of the year (Arbogast and Throne 1997). This may result in a situation where a computer

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model is being used to simulate growth for a considerable length of time under conditions for which little or no data were available to develop the model (Weaver and Throne 1994). This causes concern because simulation studies have shown that small changes in development or survival rates can have a large impact on the size of subsequent populations (Throne 1989).

Several studies on the life history of *S. cerealella* have been reported (Koone 1952, Grewal and Atwal 1967, Shazali and Smith 1985). However, these studies were carried out under various environmental and diet conditions and did not include extreme environmental conditions. Therefore, this study was conducted to determine survivorship and duration of immature development of Angoumois grain moth on corn stored over the range of temperatures and relative humidities at which the insect can survive and develop. In addition, we report on sex ratio and weight of emerged adults. The intent was to obtain data that will be useful in developing a simulation model of *S. cerealella* population dynamics for use in optimizing pest management strategies. Data other than those reported in this study also will be required before a complete population model can be developed, such as data on adult longevity and fecundity.

Materials and Methods

Insect Cultures. There were two populations of Angoumois grain moths used in this study. They were collected from farm-stored corn at two sites in south-central South Carolina in late 1991 and early 1992, and again in late 1992 and early 1993. Laboratory populations were maintained at 25 ± 1°C, 65 ± 5% RH, and a photoperiod of 12:12 (L:D) h on 'Pioneer 3320,' a dent corn hybrid, *Zea mays* L., that was grown in the southeastern United States. The corn used for the first and second populations was from the 1991 and 1992 crops, respectively. Before use, the corn was cleaned to remove large objects and small particles, and screened through a no. 6 (3.35-mm openings) U.S. standard sieve. The corn was fumigated with phosphine shortly after purchase, stored at ≈5°C, and frozen at ≈2°C for at least 3 wk to ensure disinfestation.

Development and Survivorship. The studies were conducted at seven temperatures (10, 15, 20, 25, 30, 35, and 40°C) over four saturated salt solutions (K_2CO_3, NaBr, NaCl, and KCl). These salt solutions maintain relative humidities of 43, 53–61, 75–76, and 82–87%, respectively, over the temperature range studied (Greenspan 1977). Relative humidities reported are means of those reported by Greenspan (1977) over the range of temperatures used in this study (KCl: 84.5%; NaCl: 75.2%; NaBr: 57.7%; K_2CO_3: 43.2%). Either relative humidity or moisture content could be used as a classification factor because they are mathematically related (Throne 1994). We used relative humidity as a classification factor because it is a calculated value (can be obtained from a table; Greenspan 1977) and is not subject to measurement error. We also monitored moisture content of corn samples throughout the study (Wicklow et al. 1998). The experiments were conducted at a constant photoperiod of 12:12 (L:D) h. Development and survivorship were determined in 1992 using 1991-crop corn and the 1991–1992 moth culture. The entire experiment was repeated in 1993 using 1992-crop corn and the 1992–1993 moth culture.

Eggs. Eggs were obtained by confining newly emerged F_2 adults from the laboratory cultures in a 237-ml (one-half pint) glass jar containing an 8 by 30-cm piece of black construction paper that had been folded 11 times and stapled in the center to create a tight accordion-like oviposition substrate that was 8 by 2.5-cm wide (Ellington 1930). After confinement at culture conditions for 12 h, the adults were removed, and the oviposition substrates were unfolded. Cohorts of ≈50 eggs were cut from the paper strips and placed in 237-ml glass jars covered with copper screen and filter paper–lined lids. These jars were placed on perforated false floors over the appropriate salt solution in 28 plastic boxes (seven temperatures by four relative humidities). No additional moisture was added to the eggs during incubation. Eggs were observed twice daily for egg hatch at 25, 30, 35, and 40°C and daily at 10, 15, and 20°C until egg hatch ceased. Egg development time and eclosion rate were determined from these data.

Neonate to Adult Emergence. Four 300-g samples of corn were placed in individual cages (8 by 8 by 8.4 cm high) on a perforated false floor supported at 1.5 cm above the actual floor within covered plastic boxes (40 by 27.5 by 16 cm high). Each box contained a specific saturated salt solution below the false floor to maintain RH. The boxes were placed in an environmental chamber maintained at 25 ± 1°C and a photoperiod of 12:12 (L:D) h. The corn was equilibrated for 6 wk.

F_3 eggs were obtained from stock cultures and were incubated at 25 ± 1°C, 65 ± 5% RH, and a photoperiod of 12:12 (L:D) h. On eclosion, 25 neonates were individually reared on equilibrated corn kernels simultaneously in each of the 28 temperature–relative humidity treatments (i.e., 700 eggs total). Each larva was transferred, using a camel-hair brush, to a 12-ml translucent polyethylene vial (2.7 cm high by 2.2 cm diameter) containing two equilibrated corn kernels. Each kernel was breached using a pin to create a small hole just above the germ to facilitate larval penetration. The vials were modified with fine mesh nylon screening fixed in the lid and base to allow for air exchange and moisture equilibration. Beginning 3 wk after the larvae were transferred to kernels, infested kernels were observed daily until all adults had emerged. After emergence seemed complete, kernels in test vials were examined using X-rays (Throne 1994) for the presence of any moth stage. If the insect appeared to be dead (e.g., desiccated), the kernel was dissected to ensure life status. If, on the negatives, the insect appeared to be alive, the kernel was returned to test conditions and X-rayed periodically to determine life status. Survivorship and duration of development from neonate to adult emergence were determined

Table 1. Survivorship of immature Angoumois grain moths on corn stored at various temperatures and relative humidities

Stage	Temperature (°C)	Percent relative humidity (mean ± SD; $n = 2$)			
		43	53–61	75–76	82–87
Egg[a]	10	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	15	0.73 ± 0.11	0.80 ± 0.01	0.64 ± 0.38	0.99 ± 0.01
	20	0.95 ± 0.01	0.92 ± 0.06	0.98 ± 0.03	0.93 ± 0.02
	25	0.88 ± 0.08	0.84 ± 0.01	0.90 ± 0.05	0.92 ± 0.00
	30	0.88 ± 0.08	0.83 ± 0.00	0.88 ± 0.08	0.96 ± 0.03
	35	0.60 ± 0.07	0.71 ± 0.05	0.78 ± 0.11	0.83 ± 0.02
	40	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Neonate to Adult[b]	10	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	15	0.20 ± 0.00	0.58 ± 0.08	0.82 ± 0.03	0.48 ± 0.11
	20	0.66 ± 0.03	0.76 ± 0.11	0.76 ± 0.17	0.80 ± 0.06
	25	0.58 ± 0.08	0.78 ± 0.03	0.68 ± 0.11	0.74 ± 0.08
	30	0.52 ± 0.06	0.50 ± 0.03	0.82 ± 0.08	0.48 ± 0.06
	35	0.06 ± 0.08	0.08 ± 0.00	0.20 ± 0.11	0.10 ± 0.08
	40	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00

[a] Egg survivorship varied with temperature ($F = 6.9$; df = 4,19; $P < 0.01$) and relative humidity ($F = 4.3$; df = 3,19; $P = 0.02$); interaction was not significant ($F = 1.5$; df = 12,19; $P = 0.20$; PROC MIXED, SAS Institute 2001).

[b] Survivorship from neonate to adult varied with temperature ($F = 74.3$; df = 4,19; $P < 0.01$) and relative humidity ($F = 15.7$; df = 3,19; $P < 0.01$); interaction also was significant ($F = 3.9$; df = 12,19; $P < 0.01$) PROC MIXED, SAS Institute 2001).

from these data, as well as sex ratio and weight of emerged adults.

Data Analysis. A general linear models procedure (PROC MIXED; SAS Institute 2001) was used to test for differences in response variables (egg and larval-pupal development time and survivorship, weight of emerged adults, and sex ratio) among environmental conditions (temperatures and relative humidities). In addition, we used the SLICE option of PROC MIXED to test simple effects (SAS Institute 2001). Effects of environmental conditions on sex ratio were analyzed as the proportion of females. Deviations in sex ratio of the emerging adults from 1:1 were analyzed using a *t*-test (Zar 1999). Variances were not homogeneous for response variables, except for sex ratio of emerged adults. No eggs hatched and no adults emerged at 10 and 40°C, so variance was 0. Zero variances could not be homogenized with variances at other temperatures; therefore, survivorship data for 10 and 40°C were excluded from the general linear model analyses. The arcsine-square-root transformation was used to homogenize variances of proportion egg survivorship before analysis. There were two observations on proportion survivorship (of 50 eggs or 25 neonates) at each environmental condition, one for each year; thus, $n = 2$ for calculation of survivorship means. We report duration of immature development for each year separately, and n is based on the number of individuals that emerged at each environmental condition. The variances for egg development time were not homogeneous, but there was no apparent pattern to the variances. Therefore, egg development times were not transformed before analysis. Variances for larval-pupal survivorship were homogeneous after the removal of the 10 and 40°C data, so larval-pupal survivorship data were not transformed before analysis. Larval-pupal development time data were log-transformed before analysis. Data for weight of emerged adults was square-root-transformed before analysis. Untransformed data are reported to simplify interpretation, but analysis results are for transformed data when a transformation was used.

A number of different types of equations were fit to the data using TableCurve 2D (SYSTAT Software Inc., 2002). Selection of an equation to describe the data was based on the magnitude and the pattern of residuals, lack-of-fit tests, and R^2 values (Draper and Smith 1981). We also ensured that the shape of the curve was reasonable for describing the data. Survivorship data from 10 and 40°C were used for curve-fitting. We did not examine the behavior of the equations beyond the range of conditions at which we measured responses, and we do not recommend using the equations to extrapolate beyond our data.

Results

Egg Development and Survivorship. Proportion of egg survivorship (Table 1) varied with temperature and relative humidity; the interaction was not significant. However, the SLICE option of PROC MIXED showed that relative humidity affected survivorship only at 15°C, so we did not include relative humidity in the model. Therefore, we described egg survivorship as a function of temperature (Fig. 1; Table 2). Survivorship was most variable at the transition temperatures of 15 and 35°C.

Duration of the egg stage (Table 3) varied with temperature but not with relative humidity; the interaction was not significant. So, we described duration of egg development as a function of temperature (Fig. 2; Table 2). The shortest incubation periods occurred at 30 and 35°C, and incubation period increased as temperatures decreased below 30°C.

Larval-Pupal Development and Survivorship. The proportion of larval-pupal survivorship (Table 1) varied with temperature and relative humidity; the interaction was also significant. The SLICE option of PROC MIXED showed that relative humidity affected survivorship only at 15 and 30°C, so we did not include

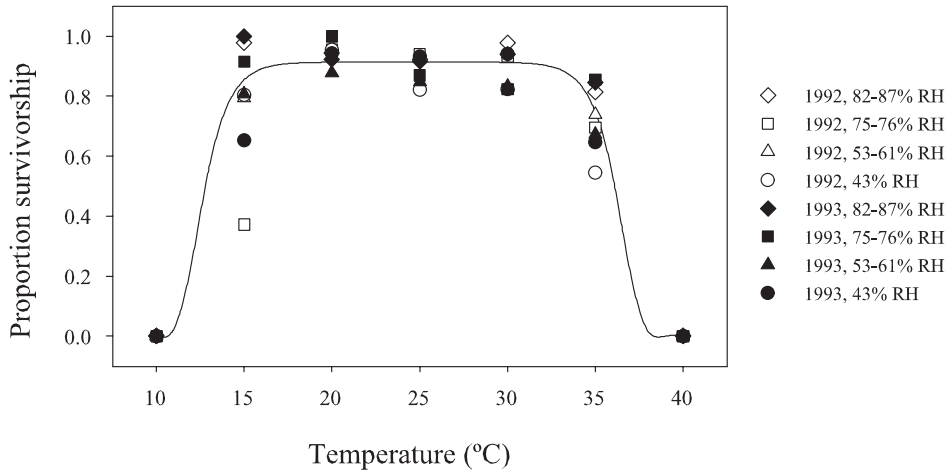

Fig. 1. Relationship between proportion of survivorship of eggs and temperature for *S. cerealella*. Solid line is from equation in Table 2.

relative humidity in the model. Therefore, we described larval-pupal survivorship as a function of temperature (Fig. 3; Table 2).

Duration of larval-pupal development (Table 3) varied with temperature and relative humidity, but not with sex. The interactions of temperature by relative humidity, temperature by sex, relative humidity by sex, and temperature by relative humidity by sex were not significant. However, the SLICE option of PROC MIXED showed that relative humidity affected larval-pupal development time only at 15 and 30°C, so we did not include relative humidity in the model. Therefore, we described larval-pupal development time as a function of temperature (Fig. 4; Table 2).

Weight of Emerged Adults. Weight of emerged adults varied only with sex ($F = 263.5$; df = 1,1; $P = 0.04$) and not with temperature ($F = 2.2$; df = 4,4; $P = 0.23$) or relative humidity ($F = 7.8$; df = 3,3; $P = 0.06$). The interactions of sex by temperature ($F = 3.7$; df = 4,4; $P = 0.12$), sex by relative humidity ($F = 1.1$; df = 3,3; $P = 0.47$), temperature by relative humidity ($F = 2.1$; df = 12,10; $P = 0.13$), and temperature by relative humidity by sex ($F = 1.5$; df = 12,10; $P = 0.26$) also were not significant. Females were almost twofold heavier than males (7.27 ± 0.14 mg for females and 3.9 ± 0.08 mg for males).

Sex Ratio. The proportion of females of emerged adults did not vary significantly with temperature ($F = 1.8$; df = 4,18; $P = 0.17$), relative humidity ($F = 0.4$; df = 3,18; $P = 0.77$), or the interaction between temperature and relative humidity ($F = 0.7$; df = 12,18; $P = 0.71$). The proportion of females averaged over all treatments (0.48 ± 0.02) did not differ from 0.5 (two-tailed *t*-test; $t = -1$; df = 529; $P = 0.32$).

Discussion

We noticed some variations from year to year in immature development times and survivorship, especially at the more extreme environmental conditions, and we conducted the test over 2 yr to capture maximum variation to best simulate field conditions. These observed differences may be caused by slight differences in conditions in the two tests: to differences in the insects, which were newly collected from the field each year; to differences in the corn used to rear the

Table 2. Equations describing effects of temperature on development and survivorship of immature Angoumois grain moths on corn

Equation	Equation parameters ± SE			Fit[a]		Lack of fit		
	a	b	c	R^2	Maximum R^2	*F*	df	*P*
Egg survivorship[b]	-0.09242 ± 0.02	$-1.25 \times 10^{-16} \pm 3.2 \times 10^{-17}$	-213886 ± 152687	0.95	0.95	1.6	4,49	0.20
Egg duration[c]	1.24 ± 0.04	119.0 ± 2.6	-	0.98	0.99	2.7	3,35	0.06
Neonate to adult survivorship[b]	-0.3372 ± 0.04	$-8.47 \times 10^{-16} \pm 2.4 \times 10^{-16}$	-267492 ± 328237	0.81	0.87	5.3	4,49	<0.01[d]
Neonate to adult duration[e]	-219 ± 48.0	6.3 ± 1.3	65312 ± 7117	0.85	0.85	0.26	2,34	0.77

[a] R^2 is the amount of variation explained by the given equation; maximum R^2 indicates the maximum amount of variation that any equation fit to the data could explain, given the pure error in the data (Draper and Smith 1981).

[b] Equation is $\ln(y) = a + be^x + ce^{-x}$, where x = temperature (°C) and y = proportion survivorship.

[c] Equation is $\ln(y) = a + b/x^{1.5}$, were x = temperature (°C) and y = incubation period (days).

[d] Although the lack of fit was significant, curves that fit the data better did not seem biologically reasonable for describing the data.

[e] Equation is $y = a + bx + c/x^2$, where x = temperature (°C) and y duration from neonate to adult emergence (days).

Table 3. Duration of immature development of Angoumois grain moth in corn stored at various temperatures and relative humidities for two tests

Stage	Temperature (°C)	Year	Percent relative humidity [mean ± SD (*n*)]			
			43	53–61	75–76	82–87
Egg[a]	15	1992	25.5 ± 1.4 (41)	26.4 ± 0.9 (39)	29.6 ± 1.9 (19)	29.1 ± 0.9 (48)
		1993	26.2 ± 2.4 (47)	26.6 ± 1.5 (38)	25.4 ± 1.5 (43)	24.7 ± 1.1 (46)
	20	1992	14.2 ± 0.9 (42)	14.1 ± 0.4 (52)	14.1 ± 0.6 (44)	13.6 ± 0.9 (51)
		1993	13.4 ± 1.1 (48)	12.6 ± 0.5 (43)	12.6 ± 0.9 (47)	12.4 ± 0.6 (48)
	25	1992	8.7 ± 0.7 (46)	8.5 ± 0.8 (45)	8.8 ± 1.4 (46)	8.3 ± 0.7 (36)
		1993	8.3 ± 0.7 (41)	8.4 ± 0.5 (39)	8.4 ± 1.8 (40)	8.2 ± 0.8 (41)
	30	1992	6.5 ± 0.8 (42)	6.6 ± 0.5 (35)	6.5 ± 0.9 (41)	6.0 ± 0.5 (45)
		1993	6.8 ± 0.5 (48)	7.0 ± 0.2 (39)	7.0 ± 0.3 (42)	7.0 ± 0.5 (48)
	35	1992	6.7 ± 0.6 (30)	6.5 ± 0.6 (51)	6.3 ± 0.8 (32)	5.8 ± 0.5 (44)
		1993	6.6 ± 0.6 (31)	6.6 ± 0.6 (33)	6.8 ± 0.8 (59)	7.8 ± 2.9 (44)
Neonate to adult[b]	15	1992	210.0 ± 46.7 (5)	173.9 ± 31.7 (16)	144.7 ± 31.0 (20)	151.3 ± 29.3 (14)
		1993	240.8 ± 16.5 (5)	136.5 ± 10.9 (13)	126.1 ± 13.8 (21)	143.6 ± 21.6 (10)
	20	1992	71.4 ± 5.3 (17)	72.4 ± 11.4 (17)	64.1 ± 13.9 (22)	64.8 ± 14.2 (21)
		1993	68.8 ± 14.5 (16)	65.7 ± 14.5 (21)	59.1 ± 10.5 (16)	66.1 ± 21.9 (19)
	25	1992	47.6 ± 13.6 (13)	39.6 ± 8.1 (19)	35.6 ± 4.2 (19)	47.8 ± 14.1 (20)
		1993	44.5 ± 6.8 (16)	43.3 ± 10.1 (20)	42.0 ± 9.7 (15)	69.1 ± 27.1 (17)
	30	1992	35.4 ± 5.1 (14)	32.4 ± 8.7 (12)	33.3 ± 13.9 (19)	45.8 ± 15.1 (13)
		1993	39.6 ± 9.7 (12)	29.9 ± 2.2 (13)	28.8 ± 5.9 (22)	73.9 ± 29.0 (11)
	35	1992	— (0)	52.0 ± 7.1 (2)	38.7 ± 4.3 (7)	81.0 ± — (1)
		1993	60.0 ± 2.6 (3)	43.5 ± 3.5 (2)	44.3 ± 5.9 (3)	56.0 ± 16.2 (4)

[a] Duration of the egg stage varied with temperature ($F = 242$; df = 4,4; $P < 0.01$), but not with relative humidity ($F = 0.2$; df = 3,3; $P = 0.91$); interaction was not significant ($F = 0.3$; df = 12,12; $P = 0.97$).

[b] Development from neonate to adult varied with temperature ($F = 141$, df = 4,4; $P < 0.01$) and relative humidity ($F = 11.5$; df = 3,3; $P = 0.04$), but not with sex ($F = 0.2$; df = 1,1; $P = 0.76$). The interactions temperature by relative humidity ($F = 2.5$; df = 12,10; $P = 0.08$), temperature by sex ($F = 0.2$; df = 4,4; $P = 0.94$), relative humidity by sex ($F = 0.8$; df = 3,3; $P = 0.56$), and temperature by relative humidity by sex ($F = 1.2$; df = 12,10; $P = 0.38$) were not significant.

insects for the two tests, which was from two different crop years, although of the same variety and grown in the same region; and to differences because of unknown interactions with naturally occurring fungi specific to particular conditions as identified by Wicklow et al. (1998). Koone (1952) reported that the incubation period of eggs and the duration of the larval-pupal period of *S. cerealella* varied with the maturity of the corn used. Villacis et al. (1972) showed that the number of eggs laid, duration of immature development, and the weight and number of progeny produced by *S. cerealella* was correlated with the protein, sugar, and fat content of the corn. Thus, the differences observed in immature development and survivorship may have been related to differences in the maturity, chemistry, and possibly the specific microflora of the two lots of corn. Alternatively, the insects trapped at these field sites during 1992 and 1993 may have been from populations with different genetic composition.

No eggs hatched and no neonates survived to the adult stage at 10 or 40°C, and the incubation period of eggs and the larval-pupal development period were longer at low temperatures. *S. cerealella* can complete its life cycle at 15 and 35°C, although the rates of immature mortality are higher than at 20, 25, and 30°C.

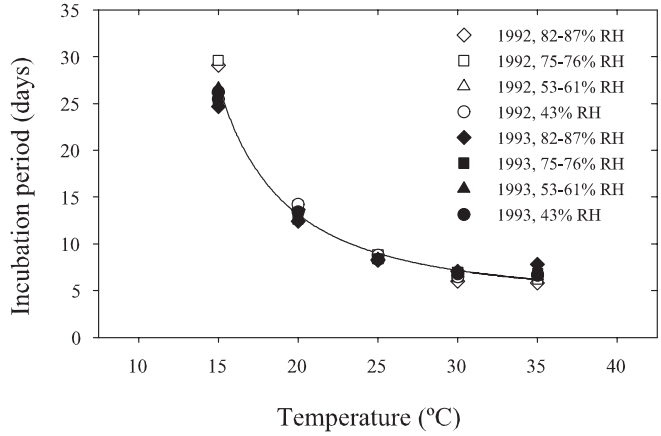

Fig. 2. Relationship between incubation period of eggs and temperature for *S. cerealella*. Solid line is from equation in Table 2.

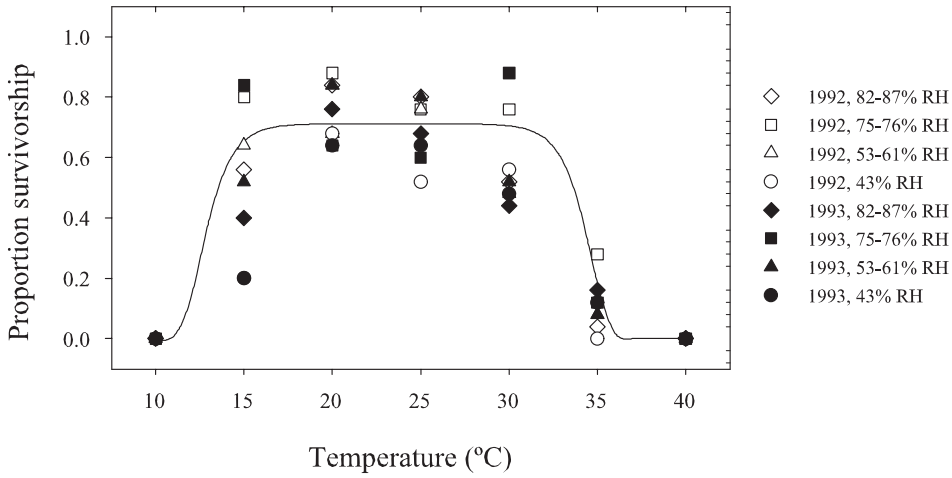

Fig. 3. Relationship between proportion of survivorship from neonate to adult and temperature for *S. cerealella*. Solid line is from equation in Table 2.

This indicates that the maximum rate of population development will occur at 25–30°C and 60–75% RH. Our measurements of survivorship may be high because we made holes in the corn kernels to facilitate penetration of the kernels by neonates. We would expect some mortality of neonates that are unable to penetrate kernels in actual storage conditions.

Survivorship was most variable at the more extreme temperatures of 15 and 35°C but was stable and high at 20–30°C. Information on immature development and survivorship at these more extreme temperatures is important to include in simulation models because control might be achieved by manipulating grain temperatures to conditions that result in reduced population growth. From a practical perspective, the lower temperatures are beneficial because they greatly increase immature development times. Thus, the data indicate that lowering grain temperature to 15°C would be a good management tool for Angoumois grain moth in stored corn, and this is a feasible option for most of the corn-growing regions of the United States (Arthur et al. 1998, 2001).

Temperature had the greatest effect on development and survivorship of immature Angoumois grain moths. Although the effect of relative humidity was sometimes statistically significant, this effect was minimal and usually most pronounced at extreme temperatures. This indicates that the effect of relative humidity is most important when the insect is already stressed because of adverse temperatures. Thus, a computer model may need to include effects of relative humidity at extreme temperatures to accurately simulate population dynamics. Validation studies will show whether this is required.

It is difficult to compare our data with those from previous studies because environmental conditions, food, and genetics of the insect populations varied among studies. Grewal and Atwal (1967) reported on duration of immature development on corn at five temperatures and three relative humidities, but they

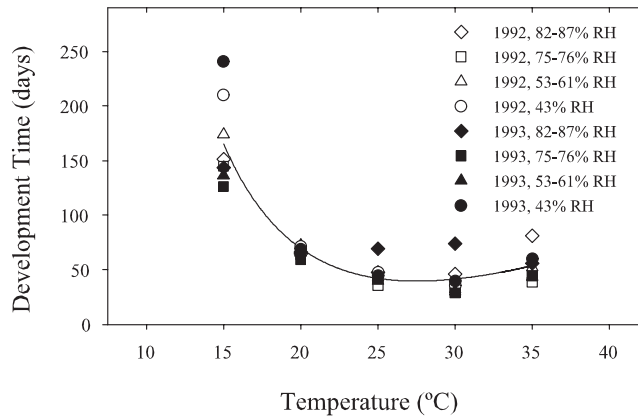

Fig. 4. Relationship between development from neonate to adult emergence and temperature for *S. cerealella*. Solid line is from equation in Table 2.

used corn kernels mixed with flour. Duration of development for both egg and larval-pupal stages was slower in our study across all temperatures and relative humidities compared with results from their study. For example, at 30°C and 60% RH, it took 4.1 and 19.8 d in their study compared with 6.8 and 31.1d in our study for duration of development for the egg and larval-pupal stages, respectively. They reported that the most suitable environmental conditions for development from egg to adult occurred at 25–30°C and 80% RH (28.1 d). Similarly, our results indicated that the best conditions for development occurred at 30°C and 75% RH (30.9 d). Survival at 25°C and 60% RH during both the egg stage and through immature development was higher in our study (84 and 78%, respectively) compared with their data (79.5 and 47.5%, respectively). The study by Shazali and Smith (1985) on sorghum also indicates longer immature development times than reported by Grewal and Atwal (1967). In the study by Shazali and Smith (1985), the optimum conditions for immature development also were found to be 25–30°C and 60–80% RH.

We found no differences in duration of immature development for the two sexes across all temperatures and relative humidities. Similarly, sex did not affect the duration of immature development in other stored-product insects (Satomi 1960, Throne 1994). Therefore, sex does not need to be included as a factor when modeling development of immature Angoumois grain moth.

A 1:1 sex ratio in our study is similar to that reported by Pandey and Pandey (1976) for growth and development of *S. cerealella* on different varieties of corn in laboratory conditions. Gerdin and Heinrichs (1986) also reported that the number of emerged females in relation to males reared on different rice cultivars was between 1:1–1.5:1 during four generations.

The weight of emerged males and females in our study is similar to the weight of males and females reported by Peters et al. (1972) in moths reared on corn with different levels of amylose. Ismail et al. (1988) also found a similar variation of weight of emerged males and females that were reared on wheat under different light regimens.

Although the ideal environmental conditions for *S. cerealella* growth and development lie within the range of 25–30°C and 60–75% RH, the ability of this insect to complete development at 15 or 35°C and 43% RH enables this pest to infest stored grain not only in tropical and subtropical climates but also in cooler climates. Our results can be used to determine the optimal storage conditions for avoiding Angoumois grain moth damage and to assess relative damage potential as a function of temperature. It is obvious that corn stored below 15°C would not be conducive to Angoumois grain moth development.

Our data can be used to develop a computer model for simulating population dynamics of immature Angoumois grain moth in corn. However, adult survivorship and fecundity data are still required before a simulation model can be developed for optimizing Angoumois grain moth management strategies in stored corn.

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References Cited

Agrawal, R. K., A. K. Bhardwaj, P. K. Srivastava, and K. N. Singh. 1977. Pre-harvest infestation of wheat by grain moth and rice weevil. Indian J. Entomol. 39: 357–360.

Arbogast, R. T., and M. A. Mullen. 1987. Dynamics of *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae) and *Sitophilus zeamais* Motschulsky (Coleoptera: Curculionidae) populations in a small bulk of stored corn. Res. Popul. Ecol. 29: 1–15.

Arbogast, R. T., and J. E. Throne. 1997. Insect infestation of farm-stored maize in South Carolina: towards characterization of a habitat. J. Stored Prod. Res. 33: 187–198.

Arthur, F. H., J. E. Throne, D. E. Maier, and M. D. Montross. 1998. Feasibility of aeration for management of maize weevil populations in corn stored in the southern United States: model simulations based on recorded weather data. Am. Entomol. 44: 118–123.

Arthur, F. H., J. E. Throne, D. E. Maier, and M. D. Montross. 2001. Impact of aeration on maize weevil (Coleoptera: Curculionidae) populations in corn stored in the northern United States: simulation studies. Am. Entomol. 47: 104–110.

Bitran, E. A., T. B. Campos, and D. A. Oliveira. 1978. Avaliacão experimental de danos causados por pragas em milho armazenado em condicões confinadas. II- *Sitotroga* cerealella (Olivier, 1819) (Lepidoptra: Gelechiidae). Arq. Inst. Biol. 45: 251–260.

Cogburn, R. R. 1974. Domestic rice varieties: Apparent resistance to rice weevils, lesser grain borers, and Angoumois grain moths. Environ. Entomol. 3: 681–685.

Draper, N. R., and H. Smith. 1981. Applied regression analysis, 2nd ed. Wiley, New York.

Ellington, G. W. 1930. A method of securing eggs of the Angoumois grain moth. J. Econ. Entomol. 23: 237–238.

Gerdin, M. P., and E. A. Heinrichs. 1986. Grain damage and development of the Angoumois grain moth *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae) on rice as influenced by cultivars and grain characteristics. J. Plant Prot. Tropics. 3: 81–93.

Greenspan, L. 1977. Humidity fixed points of binary saturated aqueous solutions. J. Res. Natl. Bur. Stand. A81: 89–96.

Grewal, S. S., and A. S. Atwal. 1967. The influence of temperature and humidity on the development of *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae). J. Res. 6: 353–358.

Howlader, A. J., and S.M.A. Matin. 1988. Observations on the pre-harvest infestation of paddy by stored grain pests in Bangladesh. J. Stored Prod. Res. 24: 229–231.

Imura, O., and R. N. Sinha. 1984. Effect of infestation by *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae) and *Sitophilus oryzae* (Coleoptera: Curculionidae) on the deterioration of bagged wheat. Environ. Entomol. 13: 1471–1477.

Ismail, I. I., A.K.M. El-Nahal, A. H. Kamel, and T. S. Mostafa. 1988. Effect of light on the development of the

Angoumois grain moth *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae). Insect Sci. Appl. 9: 27–29.

Koone, H. D. 1952. Maturity of corn and life history of the Angoumois grain moth. J. Kans. Entomol. Soc. 25: 103–105.

Pandey, V., and N. D. Pandey. 1976. Growth and development of *Sitotroga cerealella* (Olivier) on different varieties of maize. Indian J. Entomol. 38: 125–129.

Peters, L. L., M. L. Fairchild, and M. S. Zuber. 1972. Effect of corn endosperm containing different levels of amylose on Angoumois grain moth biology. 1. Life cycle, certain physiological responses, and infestation rates. J. Econ. Entomol. 65: 576–581.

SAS Institute. 2001. The SAS System for Windows, Release 8.02. SAS Institute, Cary, NC.

Satomi, H. 1960. Differences in some physiological and ecological characters between two allied species of the rice weevils, *Calandra oryzae* and *C. sasakii* collected from different districts of the world. Jpn. J. Ecol. 10: 218–226.

Seifelnasr, Y. E., and R. B. Mills. 1985. Resistance of pearl millet cultivars to *Sitophilus* oryzae, *Sitotroga cerealella*, and *Rhyzopertha dominica.* J. Econ. Entomol. 78: 181–184.

Shazali, M.E.H., and R. H. Smith. 1985. Life history studies of internally feeding pests of stored sorghum: *Sitotroga cerealella* (Ol.) and *Sitophilus oryzae* (L.). J. Stored Prod. Res. 21: 171–178.

Singh, V. S., S. K. Bhatia, and H. C. Bansal. 1977. Susceptibility of barley to *Sitotroga* cerealella (Olivier) infestation and their effect on insect's development. Bull. Grain Tech. 15: 95–99.

Singh, K. N., R. K. Agrawal, and P. K. Srivastava. 1978. Infestation of grain moth *Sitotroga* cerealella Oliv. and maize weevil *Sitophilus zeamais* Mots. on standing crops in the field. Bull. Grain Tech. 16: 125–127.

Storey, C. L., D. B. Sauer, O. Ecker, and D. W. Fulk. 1982. Insect infestation in wheat and corn exported from the United States. J. Econ. Entomol. 75: 827–832.

SYSTAT Software Inc. 2002. TableCurve 2D version 5.01. SYSTAT Software Inc., Richmond, CA.

Throne, J. E. 1989. Effects of noncatastrophic control technologies that alter life history parameters on insect population growth: a simulation study. Environ. Entomol. 18: 1050–1055.

Throne, J. E. 1994. Life history of immature maize weevils (Coleoptera: Curculionidae) on corn stored at constant temperatures and relative humidities in the laboratory. Environ. Entomol. 23: 1459–1471.

Throne, J. E. 1995. Computer modeling of the population dynamics of stored-product pests, pp. 169–195. *In* D. S. Jayas, N.D.G. White, and W. E. Muir (eds.), Stored-grain ecosystems. Marcel Dekker, New York.

Villacis, J. S., C. M. Sosa, and A. C. Ortega. 1972. Comportamiento de *Sitotroga cerealella* Olivier (Lepid: Gelechiidae) en diez tipos de maiz con caracteristicas contrastantes. Rev. Per. Entomol. 15: 153–163.

Weaver, D. K., and J. E. Throne. 1994. Life history data for *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae) in farm-stored corn and the importance of sub-optimal environmental conditions in insect population modeling for bulk commodities, pp. 599–603. *In* E. Highley, E. J. Wright, H. J. Banks, and B. R. Champ (eds.), Proceedings of the 6th International Working Conference on Stored-Product Protection. Canberra, Australia, CAB International, Wallingford, United Kingdom.

Weston, P. A., and P. L. Rattlingourd. 2000. Progeny production by *Tribolium castaneum* (Coleoptera: Tenebrionidae) and *Oryzaephilus surinamensis* (Coleoptera: Silvanidae) in maize previously infested by *Sitotroga cerealella* (Lepidoptera: Gelechiidae). J. Econ. Entomol. 93: 533–536.

Wicklow, D. T., D. K. Weaver, and J. E. Throne. 1998. Fungal colonists of maize grain conditioned at constant temperatures and humidities. J. Stored Prod. Res. 34: 355–361.

Zar, J. H. 1999. Biostatistical analysis. Prentice Hall, Upper Saddle River, NJ.

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